DEVELOPMENTAL CHANGES IN THE BIOENERGETICS OF DECAPOD LARVAE

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Anger, K. 1991 09 01: Developmental changes in the bioenergetics of decapod larvae. *Memoirs of the Queensland Museum* 31: 289–308. Brisbane. ISSN 0079-8835.

Developmental changes in bioenergetic traits of larval Decapoda are reviewed, comparing subsequent stages of a moult cycle, larval instars, or different taxa that are considered to represent a phylogenetic sequence. Recent data suggest that some developmental trends in energy partitioning might be similar on all these levels of comparison. These tendencies imply: decreasing instantaneous growth rates, increasing metabolic loss, decreasing net growth efficiency, and an increasing dependence on energy reserves accumulated in earlier stages of development. They are interpreted as signs of an increasing degree of lecithotrophy in late stages of a moult cycle, late instars of larval development, or in evolutionary advanced taxa within a phylogenetic sequence, respectively. Biochemical changes suggest a developmental shift in predominant growth mechanisms, from hypertrophy (enlargement of average cell size during development, accumulation of lipid reserves) toward hyperplasy (increase in cell number, protein accumulation). Within a moult cycle, the latter phase becomes in principle independent of external energy supply, when a critical point (the 'point of reserve saturation', or 'D_0 threshold'), has been passed. Such a bioenergetic transition, from a phase of energy accumulation to one of epidermal reconstruction, can occur also between successive instars of development: in hermit crab development, the megalopa reaches metamorphosis exclusively with energy accumulated by preceding instars. This mode of development, termed secondary lecithotrophy, is interpreted as an adaptation to extremely specialised habitat requirements (here: a mollusc shell). In the sequence Caridea–Astacidea–Anomura–Brachyura, there is an increasing trend in the average carbon/nitrogen ratio of larvae. This suggests an evolutionary tendency in the larval development of the Decapoda toward an increasing lipid content and possibly, increasing degrees of secondary lecithotrophy and habitat specialisation. It corresponds with decreasing trends in the number and variability (the latter both in relation to number and morphology) of larval instars, and an increasing degree of morphological change during development. □ *Crustacea, Decapoda, larval development, moult cycle, bioenergetics, growth mechanisms.*

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The bioenergetics of an organism can be defined through the construction of an energy budget that quantifies the fate of nutritional energy (Ivlev, 1945; Warren and Davis, 1967; Welch, 1968). The partitioning among the major energy flows (tissue and exuvia production, respiratory and excretory losses) in crustaceans is illustrated in a schematic diagram that treats these flows as black boxes (Fig. 1). While bioenergetic aspects have been studied in great detail in adult Crustacea, those of their larval stages are much less known. In the present review, I summarise recent advances in our efforts to open in larval decapod crustaceans those black boxes, and so understand in more detail how they function internally, how they are connected among each other, and how such bioenergetic traits may change during development.

Only two decades ago, virtually nothing was known about uptake and partitioning of nutritional energy in decapod larvae reared under controlled conditions in the laboratory. First quantitative data on feeding and growth were published by Reeve (1969) and Regnault (1969), who studied caridean shrimp larvae. Respiration rates had already been measured by Zeuthen (1947) in an unidentified zoea larva, and later by an increasing number of authors in various larval decapod species (Schatzlein and Costlow, 1978).

Mootz and Epifanio (1974) presented the first fairly complete energy budget for a larval decapod, the crab *Menippe mercenaria*. This study was followed by an increasing number of others that provided more or less complete information on energy partitioning in larval prawns, lobsters, anomurans, and brachyurans (Table 1). Most of these budgets have in common that they account for only gross changes during larval development, presenting 'average' flow values for subsequent instars. However, each larval instar undergoes during its

moult cycle a number of anatomical, physiological and biochemical changes that are controlled by hormonal processes (Christiansen, 1988). Hence, a much higher temporal resolution in sampling and measuring protocols, and consequently, considerably increased experimental and analytical efforts are necessary to study changes in energy partitioning of decapod and other crustacean larvae in relation to developmental processes. The first study that explicitly related bioenergetic changes in a larval decapod to the moult cycle was published only one decade ago (McNamara *et al.*, 1980).

The moult cycle can be devided into stages and substages, for which a classification system was introduced already half a century ago by Drach (1939). However, the first detailed description of anatomical changes occurring during individual moult cycles in a larval decapod appeared only recently (Anger, 1983). This description allows the identification of the major stages of Drach's classification system, and their use as a meaningful reference basis for the analysis of physiological and biochemical changes that may be observed during the course of larval development.

The following synopsis will deal exclusively with changes in bioenergetic traits as results of developmental events, and it will be based mainly on information from a few intensively studied 'model species' such as the brachyuran crabs *Hyas araneus* and *Carcinus maenas*, and the hermit crab *Pagurus bernhardus*. In these instances, sufficient experimental data obtained under constant conditions have become available to allow some generalisations and modelling. Effects caused by external factors such as temperature, salinity, and food availability must be excluded here from this review.

THE MAJOR ENERGY FLOWS

The parameters of the energy budget (Fig. 1) are linked by the following equations, from which conversion or growth efficiencies can be derived (Ivlev, 1945; Warren and Davis, 1967; Welch, 1968):

$$G = G_T + G_E = F - L - R - U \quad \text{[eq. 1]}$$

$$A = G + R + U = F - L \quad \text{[eq. 2]}$$

$$K_1 = G/F \quad \text{[eq. 3]}$$

$$K_2 = G/A \quad \text{[eq. 4]}$$

where:
A = assimilation of energy from food

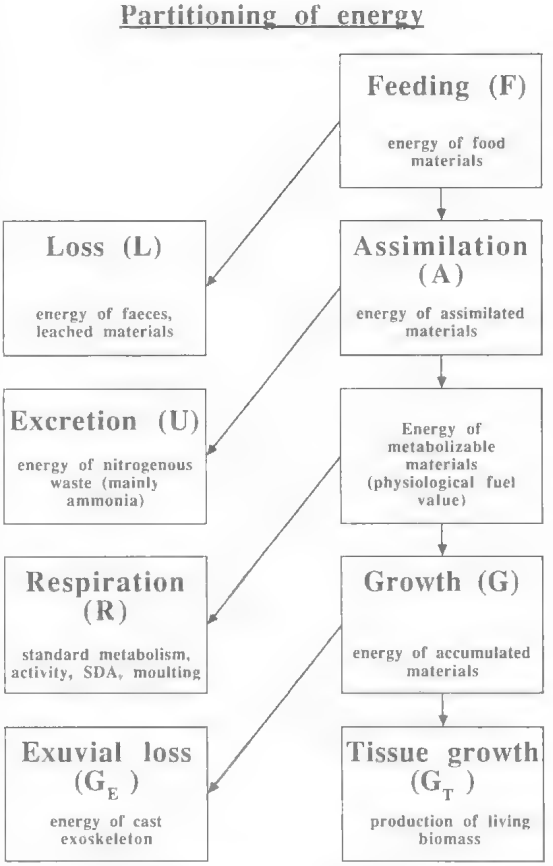

FIG. 1. Schematic diagram of energy partitioning in decapod larvae (after Ivlev, 1945; Warren and Davis, 1967; Welch, 1968).

F = food uptake
G = total body growth (briefly referred to as 'growth')
G_T = tissue growth (production of living biomass)
G_E = exuvia growth (production of cuticle materials)
K_1 = gross growth efficiency
K_2 = net growth efficiency
L = sum of losses by defaecation and leaching (loss of small particles and liquid from food, due to inefficient feeding mechanisms)
R = respiration (measured as oxygen consumption)
U = excretion of nitrogenous waste products (measured as ammonia production)

In the above form, all parameters of the budget refer to gains or losses of energy that were integrated over some period of developmental time, for instance the duration of a given moult cycle (= instar) or of complete larval development in a given species; they are expressed in energy units (Joules) per individual. Instantaneous rates of

TABLE 1. Studies on energy partitioning in larval decapod crustaceans. Taxonomical position according to Bowman and Abele (1982).

Infraorder	Family	Species	References	Remarks
Penaeioidea	Penaeidae	*Penaeus monodon*	A	1, 2, 3, 4, 5
Astacidea	Nephropidae	*Homarus americanus*	B	1
		Homarus americanus	C, D	3, 5, 6
Anomura	Paguridae	*Pagurus bernhardus*	E, F	3, 7, 8, 9
Brachyura	Xanthidae	*Menippe mercenaria*	G	1, 2, 3
		Rhithropanopeus harrisii	H	1, 2, 3, 5
	Cancridae	*Cancer irroratus*	I	1, 3
	Portunidae	*Carcinus maenas*	J	1, 2, 3, 9
	Majidae	*Hyas coarctatus*	K	2, 3, 6, 7
		Hyas araneus	L	3, 9
		Libinia ferreirae	M	3, 4, 7, 8

Remarks: 1, only cumulative budgets (average flow rates) of successive instars; 2, excretion ignored, or added to faecal losses; 3, faecal losses calculated from difference between ingestion and assimilation, or ignored; 4, energy content of larvae estimated from dry weight or ash-free dry weight (assuming a constant energy content); 5, exuvia production not considered, or data taken from literature (from other species); 6, no energy budget given, but measurements from which a partial budget may be calculated; 7, ingestion rate not measured, i.e., partitioning only of assimilated matter considered; 8, excretion data taken from literature (from other species); 9, energy content of larvae and exuviae calculated from carbon values (Salonen *et al.*, 1976). References: A, Kurmaly *et al.* (1989); B, Logan and Epifanio (1978); C, Capuzzo and Lancaster (1979); D, Sasaki *et al.* (1986); E, Anger, 1989; F, Anger *et al.* (1990); G, Mootz and Epifanio (1974); H, Levine and Sulkin (1979); I, Johns (1982); J, Dawirs (1983); K, Jacobi and Anger (1985); L, Anger and Harms (1989); M, Anger *et al.* (1989a).

energy flow, e.g. growth rate; G, will be indicated by a point above the symbol; their dimension is: Joules per individual per unit of time (h^{-1}, or d^{-1}).

Food Uptake (*F*) and Loss (*L*)

The nutrition of decapod larvae under natural conditions has been studied by few investigators (Lebour, 1922; Stickney and Perkins, 1981; Youngbluth, 1982; Harding *et al.*, 1983; Paul *et al.*, 1990), so that we know very little about their actual food sources in the planktonic environment. These few field data as well as the overwhelming amount of laboratory observations (Harms *et al.*, 1991) suggest that most decapod larvae are omnivorous, with a general preference for zooplankton as a food source.

In larval decapods, in particular in anomuran and caridean shrimp larvae, we observed frequently a very inefficient feeding behaviour: much prey is killed but then eaten only partially. This phenomenon ('sloppy feeding') was found also in some insect larvae (Johnson *et al.*, 1975) and in carnivorous copepods (Ikeda, 1977), where it was termed 'wasteful killing' or 'over-hunting', respectively. Incomplete ingestion of prey, together with leaching of liquid and small particulate materials from food during the feeding process (Dagg, 1974; Pechenik, 1979) leads to practically uncontrollable losses and thus hampers the precise measurement of actual ingestion rates in decapod larvae. The significance of this effect will probably vary with species and stage of larval development, and with the amount, size, and quality of food.

The stage of the moult cycle has a significant influence on ingestion rates. Anger and Dietrich (1984) and Dawirs and Dietrich (1986) showed in crab larvae great daily variability of feeding activity, mostly with high values in early stages (postmoult, intermoult), and strongly decreasing figures during the premoult phase of the same instar. Repeated ex-

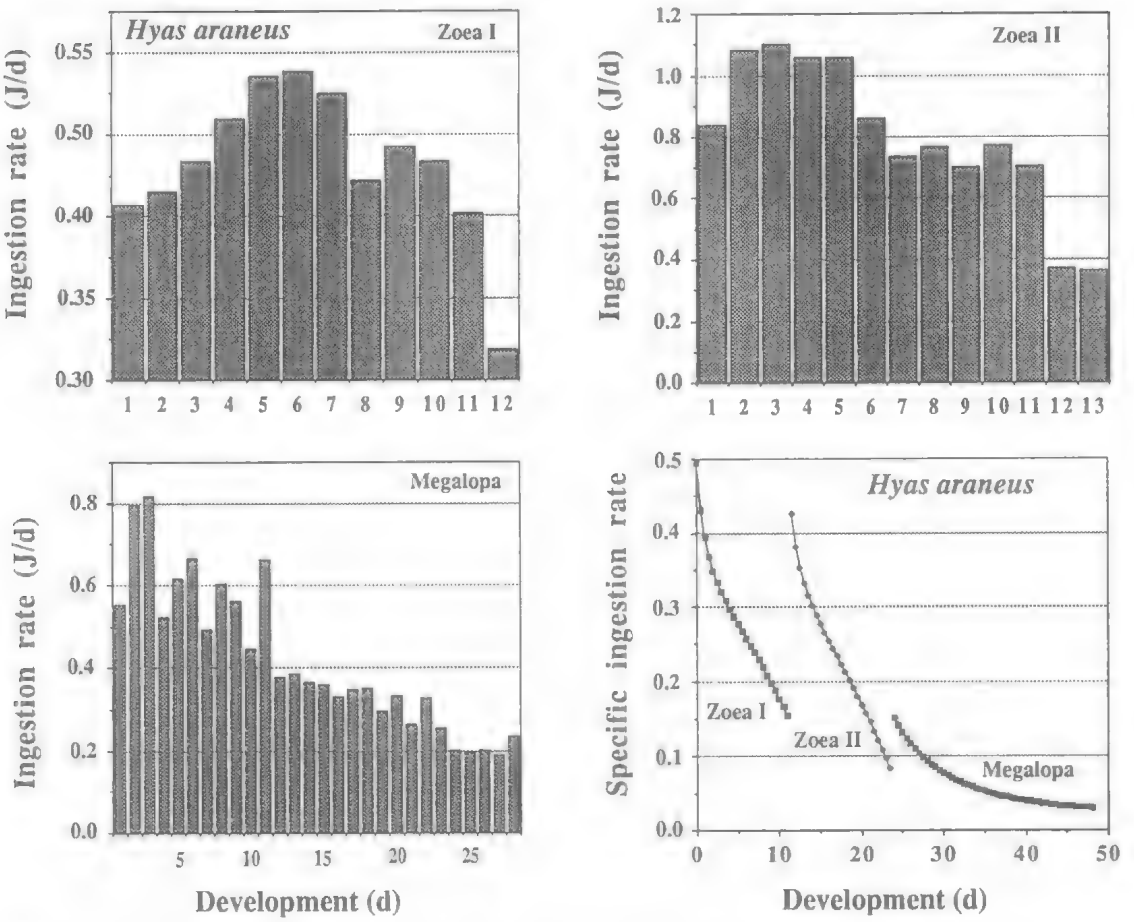

FIG. 2. *Hyas araneus*. Changes in individual and energy-specific ingestion rates during larval development (units: Joules· individual^{-1}·d^{-1}; and fraction ·d^{-1}, respectively) (data from Anger *et al.*, 1989b.)

periments with *Hyas araneus* larvae confirmed these findings, with maximum ingestion rates occurring progressively earlier in subsequent larval instars (Fig. 2). Similar patterns in $\dot{F}$ were found when phytoplankton instead of *Artemia* was given as food (Harms *et al.*, 1991), suggesting an indirect endocrine control of feeding activity via the moult cycle. In the zoeal instars of *H. araneus*, they were described with quadratic equations, in the megalopa as an exponential function of time (t) (Anger *et al.*, 1989b):

$$\dot{F}=\dot{F}_0 + a{\cdot}t - b{\cdot}t^2 \qquad \text{(zoea I, II)} \qquad \text{[eq. 5]}$$

$$\dot{F}=\dot{F}_0{\cdot}e^{-mt} \qquad \text{(megalopa)} \qquad \text{[eq. 6]}$$

The constant F_0 represents an estimate of the initial ($t = 0$) feeding rate, and the fitted parameters a, b, and m define the curvature of these functions.

When specific ingestion rates, $\dot{F}_0$/E (that is: $\dot{F}$ expressed as a fraction of larval energy content, E [both in Joules]), are plotted against time of development, decreasing values are found, not only within individual moult cycles but, on the average, also in successive larval instars (Fig. 2). According to these experiments, early spider crab zoeae may ingest up to almost one half of their own energy content per day, whereas the same instars eat much less (<20%· d^{-1}) in late premoult. The megalopa shows very low $\dot{F}$/E rates throughout the moult cycle, still decreaseing before metamorphosis (Fig. 2). However, it remains uncertain how general these patterns in decapod larvae are, until

data with a comparably high temporal resolution are available for more species.

Most 'average' ingestion rates reported in the literature (Table 1) are based on single measurements made in an unspecified stage of the moult cycle, in some cases even without specifying the larval instar. Thus, such values must be treated with much reservation, as well as gross growth and assimilation efficiencies calculated from those feeding rates (see below).

While the measurement of F suffers from great methodological difficulties, this applies even more to the determination of faecal and other losses summarised as L (Fig. 1). Consequently, most authors did not measure L directly, but estimated it from difference, F-A (eq. 2). Since measurements of F are not precise, the same must be true for indirect estimates of L. Among the authors listed in Table 1, only Logan and Epifanio (1978) determined faeces production directly in decapod larvae.

Respiration (R)

Respiration rate is usually measured as oxygen consumption (µg O_2·individual^{-1}·h^{-1}, or d^{-1}) which can then be converted to metabolic energy loss, with an equivalent of 14.06 Joules per mg O_2 (Gnaiger, 1983a). Besides integrated respiratory losses (R, in Joules per individual), I will distinguish here: (1) individual respiration rate (in µg O_2 or Joules·individual^{-1}·h^{-1} or d^{-1}), for which I will use the widely accepted symbol $\dot{V}O_2$ (instead of '$\dot{R}$'; Gnaiger, 1983b); (2) weight-specific respiration rate ($\dot{Q}O_2$; in µg O_2·individual^{-1}·h^{-1}, or d^{-1}, per unit [mg] of dry weight). The latter is a measure of the intensity of tissue metabolism. It can be expressed also as an energy-specific rate (related to energy accumulated in biomass; dimension: fraction·d^{-1}). The term 'respiration rate' will indiscriminately refer to both $\dot{V}O_2$ or $\dot{Q}O_2$. Values given in the literature represent usually an undefined rate, somewhere between basal and active metabolism, normally considered as 'routine metabolism'. This applies also to all studies listed in Table 1.

Changes of respiration during individual larval moult cycles were studied in only a few decapod species. In first-instar larvae of a freshwater prawn, *Macrobrachium olfersii*, McNamara *et al.* (1980) found slightly decreasing metabolic rates. However, this example is very specific, as these larvae reveal lecithotrophic development from the egg to the second zoeal instar. Also in the megalopa of the hermit crab *Pagurus bernhardus*, which shows secondary lecithotrophy (Anger, 1989), decreasing respiration was measured during the moult cycle (Dawirs, 1984; Anger *et al.*, 1990). Like most other decapod larvae, the zoeal instars of the hermit crab, as well as lobster (*Homarus americanus*) and crab larvae (*Hyas araneus*, *H. coarctatus*, *Libinia ferreirae*), take up food during their entire development, and their respiration increases during the course of each moult cycle (Sasaki *et al.*, 1986; Jacobi and Anger, 1985; Anger *et al.*, 1989a, b). No general correlation, however, was found between metabolism and feeding rate (Anger *et al.*, 1989b) or activity of digestive enzymes (Hirche and Anger, 1987; Harms *et al.*, 1991).

The general patterns that were found in both *Hyas araneus* and *H. coarctatus* larvae are illustrated, with the former species as an example, in Fig. 3: linear increase of respiration with time of development in the zoeal instars, but a cyclical pattern in the megalopa, with substantial increase during each ecdysis. In the zoeal instars of *Pagurus bernhardus*, a linear increase (zoea I, II), or a fairly constant respiration rate (zoea III, IV) was also measured (Anger *et al.*, 1990). Unfortunately, no data with a high temporal resolution are available for other decapod larvae, so that a generalisation of these patterns is not possible at present.

In *Hyas* spp. larvae $\dot{Q}O_2$ shows patterns of change during development that are different from those in $\dot{V}O_2$: high values after each ecdysis (postmoult) are followed by low rates throughout the intermoult and early premoult phases, and sometimes by another increase during late premoult (Fig. 3). The same patterns were observed also in larval lobsters (Sasaki *et al.*, 1986), as well as in spider crab (*Libinia ferreirae*) and hermit crab (*Pagurus bernhardus*) larvae (Anger *et al.*, 1989a, 1990). These cyclic changes in the average metabolic activity of tissues may occur generally in crustacean larvae. They should be a result of particularly energy-consuming processes of integumental growth and differentiation taking place shortly before, during, and after ecdysis (see below: mechanisms of growth).

Average $\dot{Q}O_2$ values decrease in most instances like during development from the first to the last larval instar. Only in larval lobsters was an increasing tendency observed (Sasaki *et al.*, 1986). The former trend is consistent with the general relationship of decreasing $\dot{Q}O_2$ with increasing body weight in animals (Zeuthen,

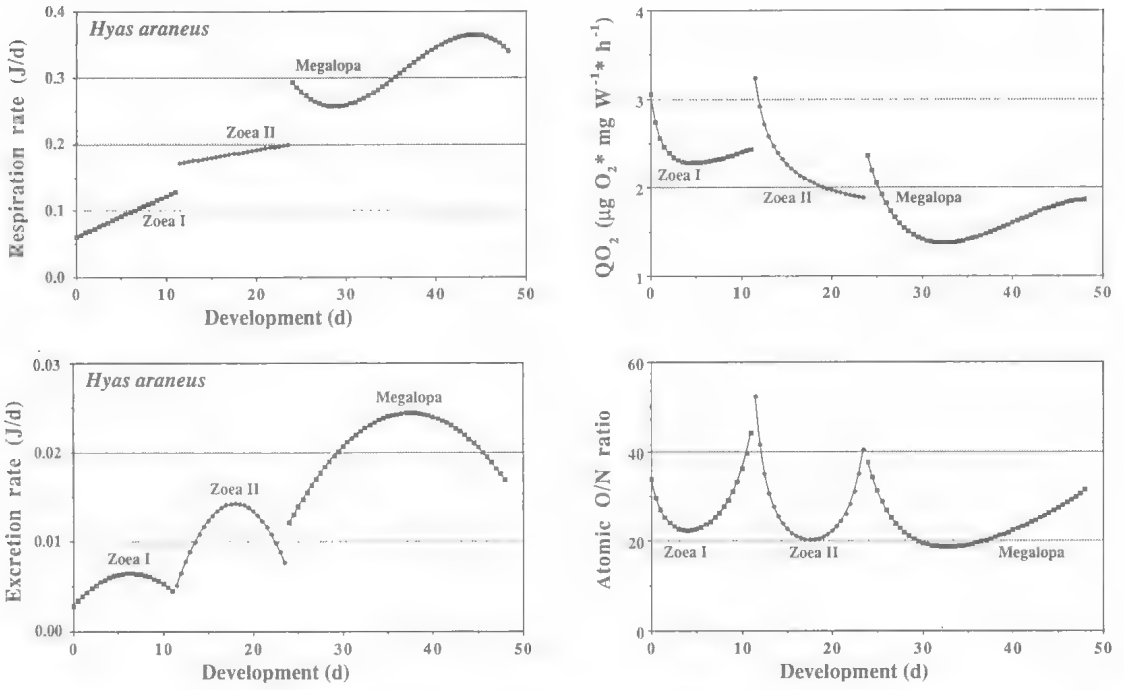

FIG. 3. *Hyas araneus*. Changes during larval development in: rates of individual respiration ($\dot{V}O_2$; *Joules* ·individual^{-1}.d^{-1}), weight-specific respiration ($\dot{Q}O_2$; µg O_2.[mg dry weight]$^{-1}$·h^{-1}), nitrogen excretion ($\dot{U}$; *Joules* ·individual^{-1}.d^{-1}), and in the atomic O/N ratio (data from Anger *et al.*, 1989b).

1947). This relationship was quantified in larvae of various decapod species (Logan and Epifanio, 1978; Schatzlein and Costlow, 1978; Anger and Jacobi, 1985). However, the patterns shown in Fig. 3 demonstrate that the respiration-weight relationship is superimposed by developmental events that are not necessarily associated with growth.

Nitrogen Excretion ($\dot{U}$)

Ammonia is assumed to be the major excretory product of larval decapods (Logan and Epifanio, 1978; Capuzzo and Lancaster, 1979; Johns, 1982). Dawirs (unpubl.) found, in addition, some traces of urea production in *Carcinus maenas* megalopa. Phosphate excretion has been measured only in some unidentified larvae isolated from plankton samples (Ikeda *et al.*, 1982; values mucher lower than in N excretion) but no data from decapod larvae maintained under controlled conditions are available. Thus, the following review will deal exclusively with the excretion of nitrogenous waste products, namely ammonia, which is assumed to represent the major part of total excretion. It can be converted to energy with a factor of 24.87 J/mg ammonia-N (Elliot and Davison, 1975).

Most investigators did not measure $\dot{U}$ as a part of the energy budget in larval decapods (Table 1). Some authors considered it as a part of faecal loss, which is not correct (it belongs to A: Fig. 1; Warren and Davis, 1967). The authors who measured it (Logan and Epifanio, 1978; Johns, 1982; Anger *et al.*, 1989b) found, however, that it constituted only a minor energy flow. In spider crab (*Hyas araneus*) larvae, we found cumulative excretory energy losses of 2–5% of A (Fig. 7). These measurements suggest that nitrogen excretion increases during larval development, not only in absolute terms (per individual) but also in relation to the other energy flows.

During individual moult cycles, excretion curves for spider crab larvae consistently showed a maximum approximately in the middle (intermoult and early premoult stages) of the moult cycle (Fig. 3). Since almost no comparable information is available from other taxa, it is not known if these patterns are typical of brachyuran larvae. Data given by Sasaki *et al.* (1986) suggest that at least larval lobsters may

exhibit quite different patterns, with low excretion rates in intermoult.

O/N Ratio

The atomic O/N ratio may be used as an indicator of the relative significance of protein as an energy source (Mayzaud and Conover, 1988). Capuzzo and Lancaster (1979) and Sasaki *et al.* (1986) found lower O/N ratios in stage IV lobsters than in earlier instars, suggesting an increasing protein catabolism during larval development. Decreasing average values were also observed during the development of spider crab larvae, however, superimposed by variation during individual moult cycles (Fig. 3). According to these data, protein catabolism in *Hyas araneus* larvae is at a maximum during intermoult, whereas lipid and/or carbohydrates play a major role in the premoult and postmoult stages.

Growth (G)

Larval growth has been studied in many decapod species (Kurata, 1962; Rice, 1968; Hartnoll, 1982; Gore, 1985; McConaugha, 1985), but different units of measurement have been used: size, moult cycle duration, fresh weight, dry weight, ash-free dry weight, carbon, nitrogen, hydrogen, protein, lipid, or energy (measured by microcalorimetry or estimated from biochemical or elemental composition).

Dawirs (1981, 1983), Anger and Dawirs (1982), and Sasaki *et al.* (1986) showed that fresh weight is a very poor measure of growth in crustaceans, as it does not reflect actual changes in living biomass during development or in relation to nutritional conditions. It should never be used as a reference unit for biochemical data (although some authors did this). Dry weight and ash-free dry weight are certainly better measures of biomass. Carbon and nitrogen measurements proved to be especially accurate and reproducible. They show highly significant relationships with the energy content (Salonen *et al.*, 1976) and with the major biochemical components, protein and lipid (Anger and Harms, 1990). These different measures of biomass can be converted into each other, either using such empirical relations or a stoichiometric model (Gnaiger and Bitterlich, 1984).

Not only different measures of biomass have been used, but also conflicting models of growth. Probably the most frequently used is 'Dyar's rule' or 'Brook's law' (Kurata, 1962). It describes an increase in size or biomass as an exponential function of the number of instars; however, several authors used it to describe growth as a function of time. Empirical data on instantaneous growth rates (see below) show that this is an erroneous use of the exponential model.

Anger and Dawirs (1982) expressed zoeal biomass in *Hyas araneus* (dry weight, C, N, H, or energy [µg or Joules· individual^{-1}]; in the latter case is: biomass = E) as a power function of time (t; [d]) within a given instar:

$$E = E_0 \cdot (t+1)^m \qquad \text{[eq. 7]}$$

E_0 is an estimate of initial ($t = 0$) energy, and m is a fitted constant (the regression coefficient of the linearized form of the equation). This model was later applied also to other larval brachyurans, *Carcinus maenas* (Dawirs, 1983), *Hyas coarctatus* (Jacobi and Anger, 1985), *Inachus dorsettensis* (Anger, 1988), *Liocarcinus holsatus* (Harms, 1990), and lobsters, *Nephrops norvegicus* (Anger and Püschel, 1986).

Another model, a second-order polynomial equation, was applied to describe megalopa growth in *Hyas* spp., where biomass reaches a maximum in the middle of the moult cycle and then decreases, prior to metamorphosis (Anger and Jacobi, 1988; Jacobi and Anger, 1985).

$$E = E_0 + a \cdot t - b \cdot t^2 \qquad \text{[eq. 8]}$$

E_0 (as in eq. 7), a, and b are fitted constants. Dawirs *et al.* (1986) suggested that this model might be better suited than eq. 7 for describing zoeal growth patterns, since they observed in *Carcinus maenas* zoeae a decrease in biomass during late premoult. The same was found also in the zoeal instars of the anomuran crabs *Pagurus bernhardus* (Anger, 1989; Anger *et al.*, 1990) and *Galathea squamifera* (Anger, unpubl.), and in the larvae of the European lobster, *Homarus gammarus* (Messerknecht, pers. comm.).

Both models predict that growth rate (G, defined as change of biomass per unit of time, that is the first derivation of eqs. 7 and 8, respectively) will decrease during each larval instar:

$$G = dE/dt = E_0 \cdot m \cdot (t+1)^{m-1} \qquad \text{[eq. 9]}$$

$$G = dE/dt = a - 2bt \qquad \text{[eq. 10]}$$

G has the dimension [Joules·individual^{-1}·d^{-1}]. Eq. 9 gives a hyperbolic, eq. 10 a linear pattern of decrease (Fig. 4). Further data from more species is required to decide which model is a better description of larval growth patterns, if a universal pattern exists. The parabola-shaped bi-

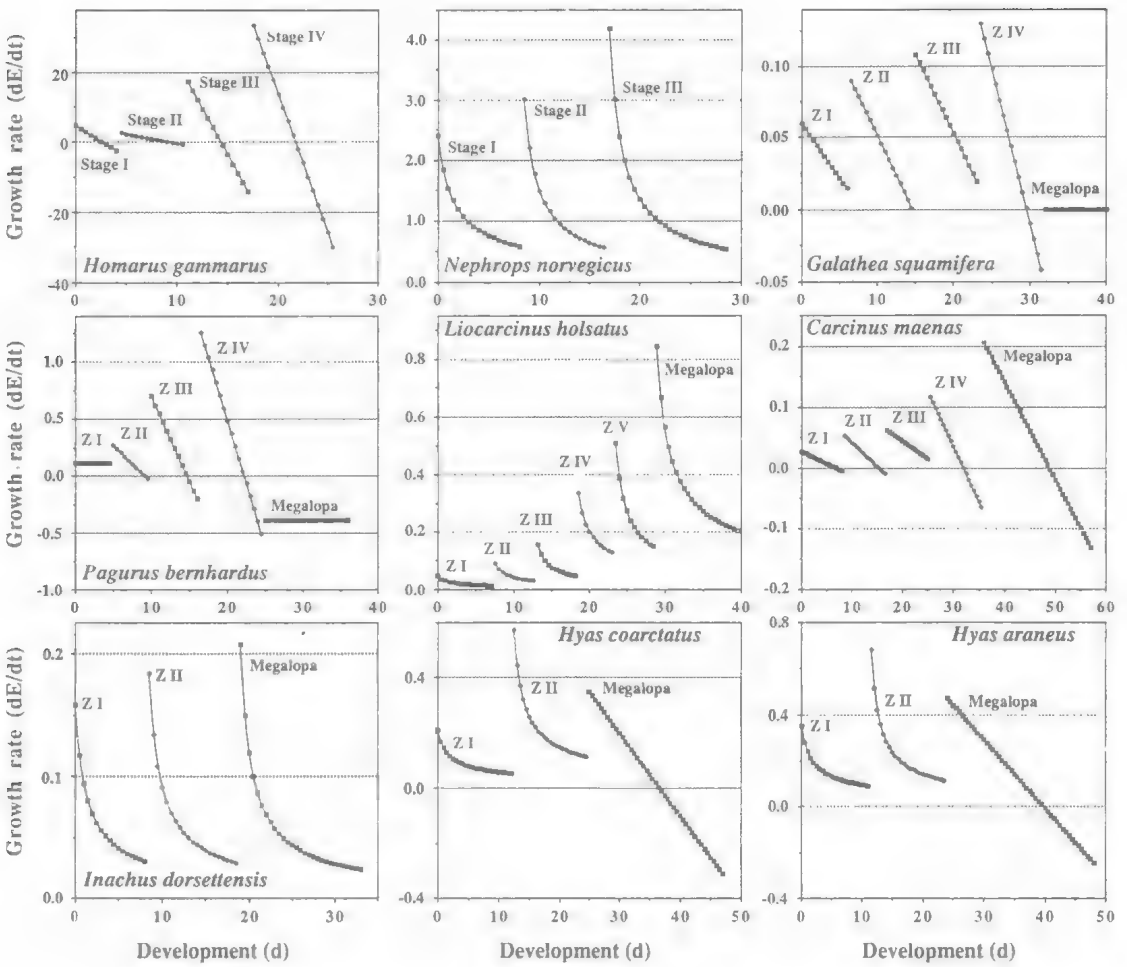

FIG. 4. Changes in individual growth rates (G, Joules ·individual^{-1}· d^{-1}) of decapod crustacean species during larval development. (sources of data: Messerknecht, pers. comm. (*Homarus gammarus*); Anger and Püschel, 1986 (*Nephrops norvegicus*); Anger, unpubl. (*Galathea squamifera*); Anger *et al.*,1990 (*Pagurus bernhardus*); Harms, 1990 (*Liocarcinus holsatus*); Dawirs *et al.*, 1986 (*Carcinus maenas*); Anger, 1988 (*Inachus dorsettensis*); Jacobi and Anger, 1985 (*Hyas coarctatus*); Anger *et al.*, 1989b, Anger and Harms, 1989 (*H. araneus*)).

omass curve (with a final decrease) described by eq. 8 might be an artifact (although I do not consider this very likely) that could be caused by weak, slow-growing larvae that are proportionally more frequent in samples taken very late (after the onset of moulting) from a culture.

Although the curvature of growth curves may remain uncertain, Fig. 4 shows one universal tendency in all nine decapod species and in a total of 34 (out of 37) instars considered: larval growth decreases during the course of individual moult cycles. Only in the zoea I and megalopa of *Pagurus bernhardus* and in the megalopa of *Galathea squamifera*, was a linear change in biomass, i.e. a constant growth rate ($\dot{G}$), found (a negative value in the secondarily lecithotrophic hermit crab megalopa); in no case was an increase observed in $\dot{G}$.

This is important to note, as some authors attempted to estimate 'average' growth rates in plankton populations of decapod larvae, applying an exponential model (see above) that predicts a progressively increasing $\dot{G}$ with time of development (Incze *et al.*, 1984; Lindley, 1988; Paul *et al.*, 1990). Since this model describes only gross biomass changes in a series of subsequent instars as a function of instar number, not as a function of time, it has very

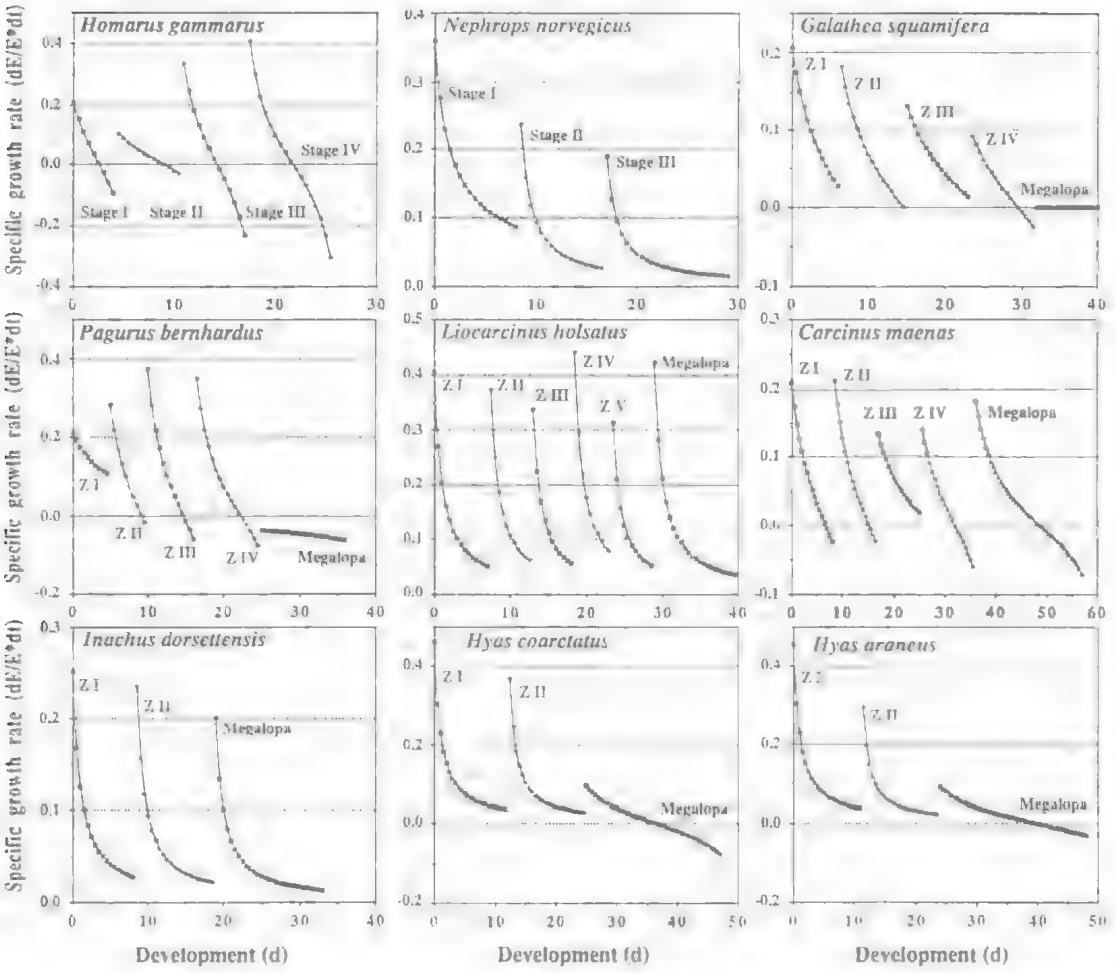

FIG. 5. Changes in energy-specific growth rates (G/E; fraction $\cdot d^{-1}$) of decapod crustacean species during larval development (sources of data: as in Fig. 4).

poor predictive power when growth within specific instars is studied. Thus, 'average' growth rates calculated from it are likely to be physiologically unrealistic (Fig. 4). Such rough estimates, however, may be useful as overall indices of growth, when only a comparison of different environmental conditions is attempted (Paul *et al.*, 1990).

Naturally, the absolute growth rate (dE/dt) depends also on the specific size of a larva: for instance, a late lobster larva may gain 100 times more energy per day than an early portunid crab larva (Fig. 4). Thus, it is useful for direct comparison to calculate specific growth rates:

$$\frac{G}{E} = \frac{dE}{E \cdot dt} = \frac{[eq.9]}{[eq.7]} \quad [eq.\ 11],$$

or

$$\frac{G}{E} = \frac{dE}{E \cdot dt} = \frac{[eq.10]}{[eq.8]} \quad [eq.\ 12],$$

respectively

Specific growth rates have the dimension of a fraction (or %) of E [d^{-1}]. Fig. 5 shows that post-moult G/E varies in most species and instars between 0.15 and 0.40 (or 15–40 %). It decreases dramatically during later moult cycle stages, often reaching negative values. The average level of daily specific growth in subsequent larval instars remains constant or it decreases. In no moult cycle or series of instars were increasing rates observed.

Crustacean growth is further complicated by a partial independence of the moult cycle from morphogenesis and growth (McConaugha, 1985). This is particularly obvious in caridean shrimp larvae, where moulting frequency may remain unaltered under suboptimal conditions, while morphogenesis and growth cease, resulting in a highly variable number and morphology of larval instars (Reeve, 1969; Knowlton, 1974).

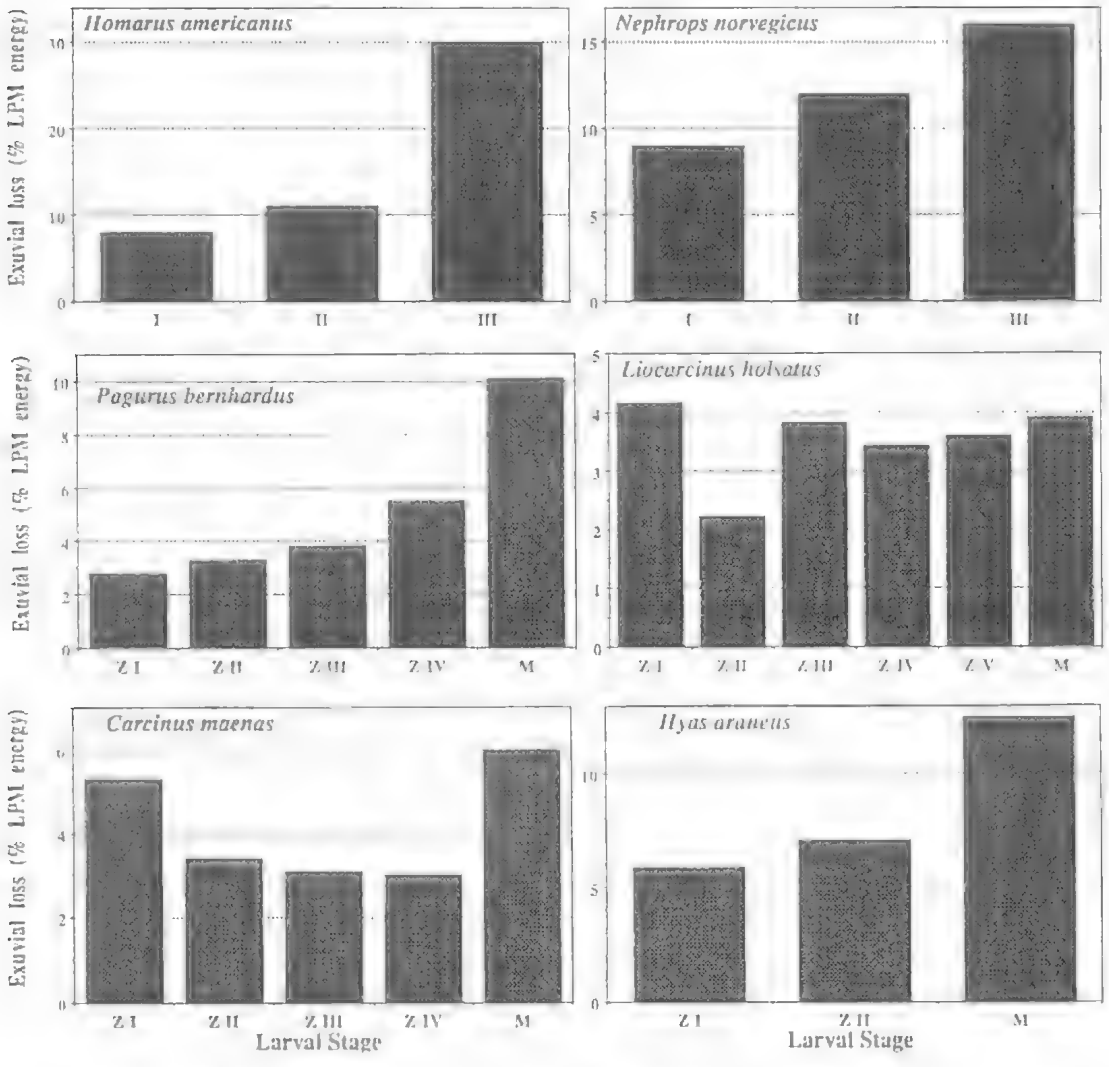

FIG. 6. Exuvial loss (% of late premoult, LPM, energy) in successive larval instars of decapod crustaceans; Z I, II etc.= zoeal stages; M= megalopa, (sources of data: Logan and Epifanio, 1978 (*Homarus americanus*), Dawirs, 1983 (*Carcinus maenas*), Anger, 1989 (*Pagurus bernhardus*); others as in Fig. 4).

EXUVIA PRODUCTION (G_E)

The exoskeleton is an integral part of crustacean growth, but equally a loss, as it is cast when ecdysis occurs (Fig. 1). Like total biomass, its absolute quantity (in Joules per individual) increases in successive larval instars at an exponential rate (Anger, 1984, 1989; Harms, 1990).

In Fig. 6 data are compiled on exuvial loss in larvae of decapod species, where measurements of late premoult biomass are available as a reference basis. It shows that anomuran and brachyuran zoeae shed *c.* 3–7% of their total late premoult energy, whereas the megalopa instar, as well as lobster larvae, lose higher percentages with their exuviae. Except in portunid crab species, there is a clear increasing trend not only in absolute (per individual), but also in percentage exuvial loss of subsequent larval instars (Fig. 6).

Among the species compared in Fig. 6, *Hyas araneus* reveals intermediate G_E values. During its complete larval development it casts <6% of total energy ingested as exuvial matter (Anger and Harms, 1989), two thirds of this loss occurring in the final (metamorphic) moult from the megalopa to the juvenile crab. In relation to total

energy assimilated, the exuvial loss amounts here to 5–9% per instar (Fig. 7).

The fraction of total growth (G) that is lost as exuvial energy, increases in *Hyas araneus* larvae from 9% (zoea I) to 13% (zoea II), and eventually 35% (megalopa). Similar or higher losses were found in larval *Menippe mercenaria* (Mootz and Epifanio, 1974), *Homarus americanus* (Logan and Epifanio, 1978), *Rhithropanopeus harrisii* (Levine and Sulkin, 1979), *Carcinus maenas* (Dawirs, 1983), and *Nephrops norvegicus* (Anger and Püschel, 1986). Lower values (mostly <5%) were reported for *Cancer irroratus (Johns, 1982), Liocarcinus holsatus* (Harms, 1990), and *Pagurus bernhardus* (Anger, 1989). In general, the data reveal that G_E tends to increase during larval development both in absolute terms, and as a percentage of either late premoult biomass G

Summary Budgets and Efficiencies

Quantitative information on uptake of food (F) and on losses that occur prior to assimilation ($L = F\text{-}A$; eq. 2), is in general considered unreliable (see above). Thus, changes that may occur during development in assimilation efficiency (A/F) and gross growth efficiency (K_1; eq. 3) will not be discussed here in detail, since both indices of food conversion are seriously affected by low precision of F measurements (Pechenik, 1979). Some possible patterns of developmental change were discussed recently by Anger and Harms (1989).

For cumulative budgets of complete larval development of decapod crustaceans, Mootz and Epifanio (1974), Logan and Epifanio (1978), Levine and Sulkin (1979), Johns (1982), and Anger and Harms (1989) calculated A/F values ranging from 45–81%. Lower assimilation efficiency (22%) was found by Dawirs (1983).

Cumulative K_1 values of complete larval development were found in most species to range from 27–30% (Mootz and Epifanio, 1974; Logan and Epifanio, 1978; Levine and Sulkin, 1979; Johns, 1982; Anger and Harms, 1989), whereas Dawirs (1983) observed a cumulative K_1 of only 3% in *Carcinus maenas* larvae .

The overall partitioning of assimilated energy (A) is exemplified with data from *Hyas araneus* (Fig. 7). In this species, the portion of A that is channelled into growth (K_2) decreases in subsequent instars from 59–26%, while respiratory (R) and excretory losses (U) increase from 39–69%, and 2–5%, respectively. Within G, exuvial loss (G_E) increases in successive instars, whereas tissue production (G_T) decreases.

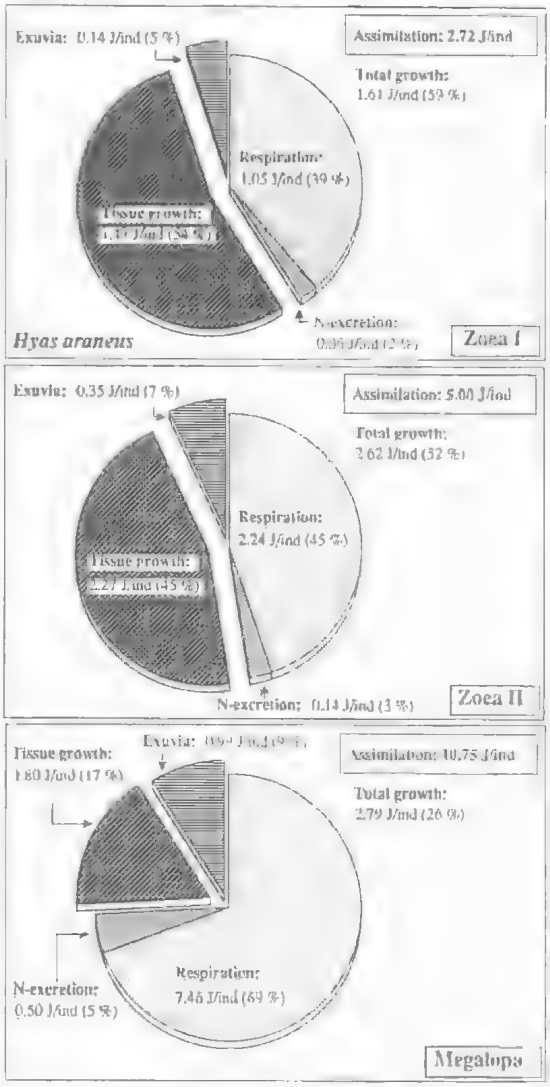

FIG. 7. *Hyas araneus*. Partitioning of assimilated energy (A) in successive larval instars (Joules, individual^{-1}, and % of A) (data from Anger *et al.*, 1989b; Anger and Harms, 1989).

With respect to changes in K_2 during larval development, some authors (compiled by McConaugha, 1985; Stephenson and Knight, 1980) found an increasing tendency from instar to instar, whereas Reeve (1969) and a number of other authors (Fig. 8) observed the opposite trend. Since K_2 decreases during larval development in most species for which sufficiently precise data with a high temporal resolution is available (Fig. 8), this may be considered more likely as a general pattern in decapod larvae.

The discrepancy between K_2 values of early

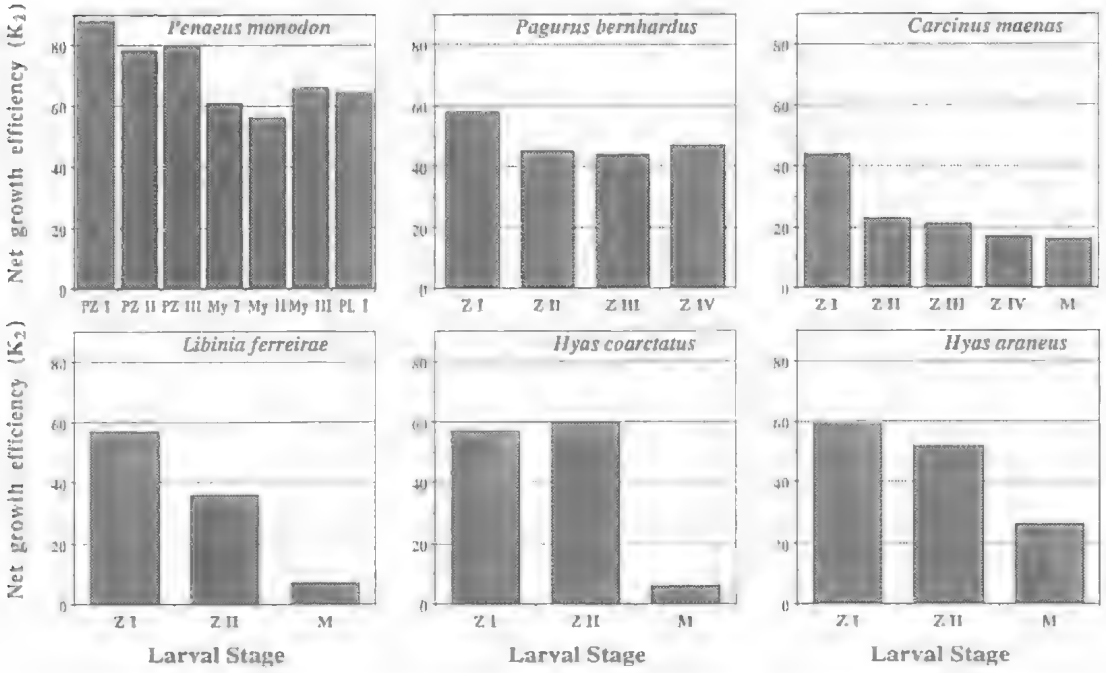

FIG. 8 Net growth efficiency (K_2; G % of A) in successive larval instars of decapod crustaceans; PZ= protozoea; My= Mysis; PL= postlarva; Z I, II etc.= zoeal stages; M= megalopa (sources of data: Kurmaly *et al.*, 1989 (*Penaeus monodon*); Dawirs,1983 (*Carcinus maenas*); Anger *et al.*, 1989a (*Libinia ferreirae*); others as in Fig. 4).

and late developmental instars appears particularly great in spider crab larvae. It is caused mainly by events that take place during the premoult (premetamorphic) phase of megalopa development, with feeding activity becoming very low (Fig. 2), and metabolic intensity of tissues remaining high (Fig. 3). As a consequence of $\dot{F}<\dot{V}O_2$, growth becomes negative ($\dot{G}<0$; Figs 4, 5). These patterns may be interpreted as signs of an increasing degree of lecithotrophy in the final instar. The ultimate degree, 'secondary lecithotrophy' (Anger, 1989), is found in hermit crab (*Pagurus bernhardus*) megalopa. No more feeding occurs here ($\dot{F}=0$), and thus development to metamorphosis depends exclusively on energy accumulated by the preceding zoeal instars. This phenomenon is associated with a switch in life style, from pelagic to benthic, and it may be interpreted as an adaptation to an extremely specialised habitat requirement, in this case the need to find a gastropod shell after settlement and metamorphosis. Secondary lecithotrophy should increase the chance to find such a particular habitat, as no time and energy must be sacrificed for feeding activity.

The degree of decrease in K_2 may thus reflect the degree of food independence, i.e. the degree of secondary lecithotrophy, in a late developmental stage. Since the ability to develop independently of food through metamorphosis should in general be more important for species that depend on very particular habitats, rather than in opportunistic settlers, the degree of lecithotrophy may represent a measure of ecological specialisation.

There is a decrease not only in average K_2 of successive larval instars (Fig. 8), but also in instantaneous values during the course of individual moult cycles (Fig. 9). The tendency of decreasing growth and K_2 values with time of development corresponds to the finding that very young, post-natal organisms tend to have particularly high net growth efficiencies (ranging from *c.* 50–80% in most poikilotherms; Calow, 1977). Each ecdysis is, in principle, comparable to hatching, i.e. to 'birth' of a larval instar, and the following moult cycle is characterised by processes of growth, morphogenesis, and physiological aging, accom-

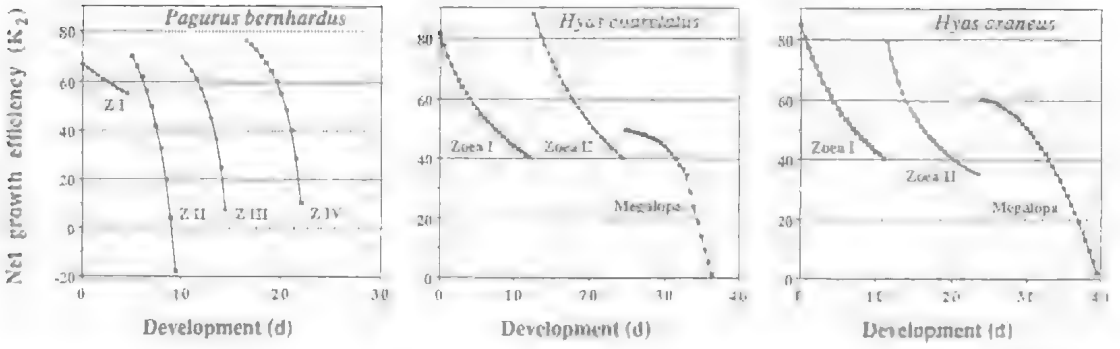

FIG. 9. Changes in instantaneous net growth efficiency (K_2) during larval development of decapod crustaceans: Z= zoeal instars (sources of data as in Fig. 4).

panied by decreasing growth efficiency. Ecdysis initiates the next cycle, beginning again with higher K_2 values (Fig. 9). Since development proceeds and the absolute age of larvae increases with each subsequent instar, a decreasing trend should be expected also in average efficiencies of successive instars. Thus, it is hypothesised that tendencies of decreasing K_2 during development (Figs 8, 9) may be a typical bioenergetic pattern in decapod larvae.

When different taxa are compared, highest average K_2 values (56–88%) were found in larvae of a penaeid prawn, lower values in anomuran zoeae (44–58%; the entirely lecithotrophic hermit crab megalopa is excluded from this comparison), and lowest in crab larvae (6–60%) (Fig. 8). It is interesting to note that this sequence might reflect a phylogenetic tendency of decreasing net growth efficiency, from more primitive toward more advanced groups (for taxonomy of Decapoda see Bowman and Abele, 1982). Since low growth efficiencies are expected in partially lecithotrophic instars or species, this would suggest a phylogenetic tendency in the Decapoda toward an increasing degree of lecithotrophy and thus, of increasing ecological specialisation. This presumption is corroborated by differences in the average chemical composition of decapod larvae belonging to different infraorders (Fig. 10; see below). However, special adaptations to environmental (including biotic) factors such as life of hermit crabs in a mollusc shell, can occur in any taxonomic group and thus, there should be many exceptions to this hypothetically postulated rule.

Mechanisms of Growth and Concluding Remarks

Available data suggest that the decreasing trends in growth rate (both per individual and per unit of biomass energy), as well as in net growth efficiency during development, may be a bioenergetic rule in larval decapods. These trends have clearly been observed during individual moult cycles (Figs 4, 5, 9), and they occur in sequences of larval instars (Fig. 8). They may be seen also in phylogenetic development, from primitive toward more advanced groups (see above: K_2). Presumably, the existence of such general patterns raises the question as to what mechanisms of growth may be involved and how these may change during larval development.

Data on elemental and biochemical composition of decapod larvae reveal recurrent patterns of developmental change that are illustrated, again with *Hyas araneus* as a well-documented example (Fig. 10). The carbon/nitrogen (C/N) ratio which is frequently used as an indicator of the lipid/protein ratio, shows here in all larval moult cycles an initial increase, followed by a transitory maximum, and a final decrease. When patterns of instantaneous growth rates in C and N are compared (dC/dt, dN/dt), the following tendencies may be discerned: (1) an initial phase with high G. It is characterised by particularly strong gain in C (i.e. lipid) and maximum C/N ratios approximately at the end of the intermoult (stage C) phase of the moult cycle. (2) The rate of accumulation in C (reflecting the lipid fraction) decreases dramatically, whereas that in N (protein) decreases more slowly. In late megalopa development, these differential slopes of instantaneous growth curves cause a reversal of biochemical patterns, with accumulation of N eventually exceeding that of C (Fig. 10).

These two distinct phases of growth correspond to those of an obligatory and a facultative

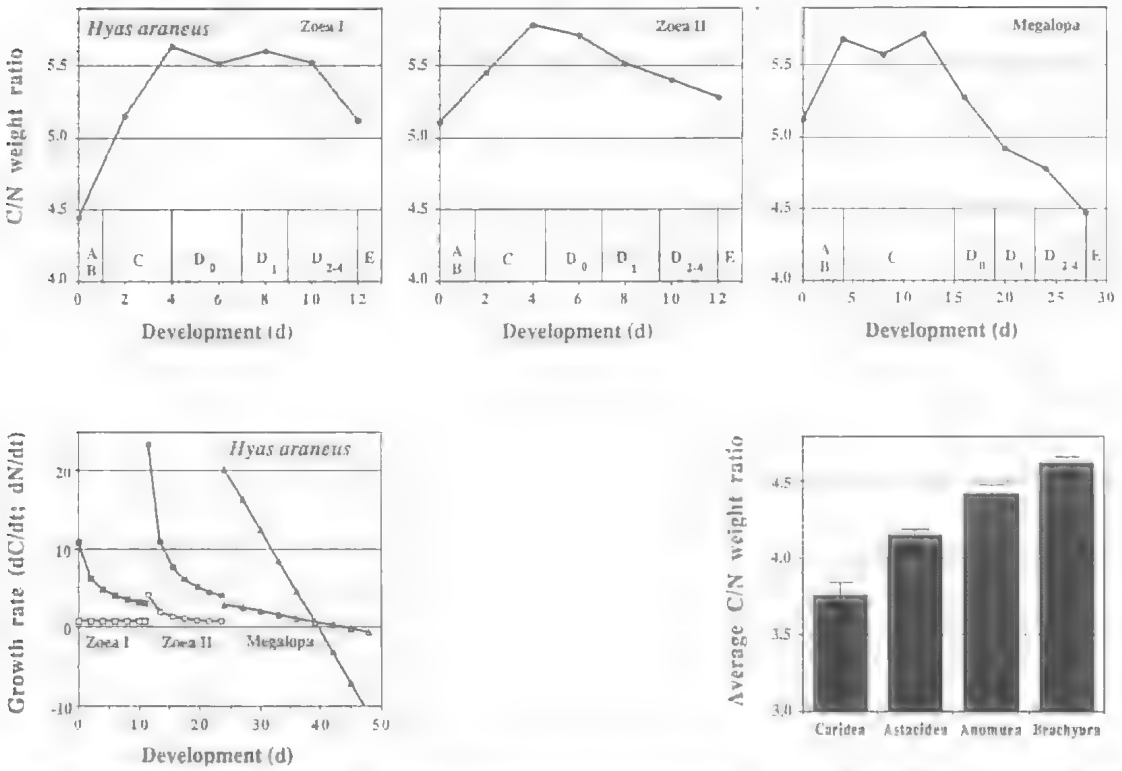

FIG. 10. *Hyas araneus*. Changes in the C/N weight ratio and in carbon- and nitrogen-specific growth rates (dC/dt, closed symbols; dN/dt, open symbols; µg individual^{-1} d^{-1}) during larval development. A–E, stages of larval moult cycles (after Drach, 1939; Anger, 1983); data from Anger and Hirche, 1990. Lower right: average C/N weight ratio (x ±95% confidence intervals) in larvae belonging to different decapod infraorders (taxonomic position after Bowman and Abele, 1982; data from 3 species of Caridea, 2 Astacidea, 2 Anomura, and 10 Brachyura after Anger and Harms, 1990).

feeding period, the latter in principle being independent of food (Anger, 1987). Thus, one can say that the final phase of the moult cycle (premoult) reveals a high degree of secondary lecithotrophy, as further development is possible with energy reserves that have been accumulated during earlier stages (postmoult, intermoult). The critical point that must be reached to allow autonomous development (the 'point of reserve saturation'; Anger and Dawirs, 1981; Gore, 1985; Dawirs, 1986), was identified as the transition between intermoult (stage C) and early premoult (stage D_0) and hence, was termed 'D_0 threshold' (Anger, 1987).

Although larvae will continue to eat when food is available, the facultative feeding period is characterised, independent of feeding conditions, by low rates of food uptake (Fig. 2) and growth (Figs 4, 5), high metabolic loss (Fig. 3), and consequently, low net growth efficieny (Fig. 9). Apparently, morphogenetic reconstruction processes and other physiological and anatomical preparations for ecdysis ('qualitative growth') have during this developmental phase priority over mere accumulation of energy ('quantitative growth'), and their completion is secured by an increased degree of lecithotrophy.

In a recent study on nucleic acids in *Hyas araneus* larvae, Anger and Hirche (1990) suggested that these two phases of growth may differ also in the relative significance of two major mechanisms of growth: cell enlargement (hypertrophy) and cell multiplication (hyperplasy). Assuming constant amounts of DNA per cell and neglecting interstitial materials, the former type of growth may be measured as an increase in the DNA content per individual, the latter as a C/DNA ratio, and synthetic activity of tissues may be indicated by the RNA/DNA ratio (Fig. 11).

Mitoses take place continuously from hatching of the zoea I to premoult of the megalopa instar, whereas maximum synthetic activity of tissues and an increase in average cell size were observed mainly in the initial (postmoult) peri-

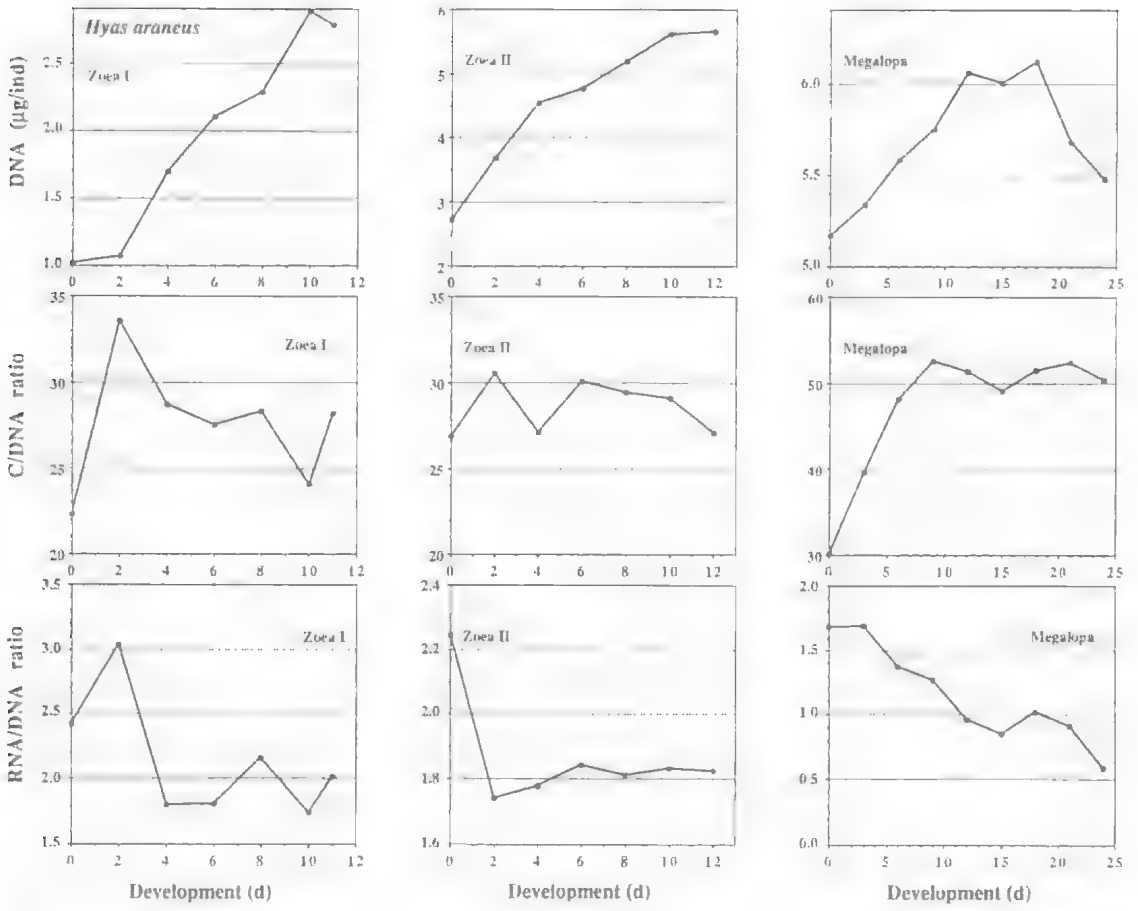

FIG. 11. *Hyas araneus*. Changes in DNA content (µg individual^{-1}), and in the carbon:DNA (C/DNA) and RNA/DNA weight ratios during larval development (data from Anger and Hirche, 1990).

ods of larval moult cycles (Fig. 11). High initial rates of synthesis are suggested also by measurements of adenosine nucleotides in *Carcinus maenas* larvae (Harms *et al.*, 1990b). They suggest a high turnover rate of ATP during postmoult and early intermoult, leading to a minimum adenylate energy charge in stage C, in spite of increasing ATP concentrations (Fig. 12). Ultrastuctural evidence (Storch and Anger, 1983), shows that this initial accumulation of energy reserves (mainly of lipids) takes place in R-cells of the larval hepatopancreas, where fat vacuoles are enlarged. Protein synthesis may be associated mainly with epidermal enlargement and reconstruction processes, and with hyperplasy rather than hypertrophy (McConaugha, 1985, and earlier papers; Freeman, 1986, 1990, 1991; Freeman *et al.*, 1983). The latter processes become independent of further external energy supply, when sufficient internal reserves of energy and essential substances have been accumulated to allow autonomous development. This energetic status is normally reached in late stage C of the moult cycle, and it may may set the signal for increasing ecdysteroid production in the larval Y-organs which then gives the stimulus for development through the premoult phase (Spindler and Anger, 1986; Anger and Spindler, 1987).

Even when food is available, the premoult stages are characterised by signs of an increasing degree of lecithotrophic development, with catabolism of lipid reserves (Fig. 10), no further increase in average cell size (Fig. 11: C/DNA), and decreasing ATP concentrations (Fig. 12). Like morphogenesis (Anger, 1987), these trends may be fairly independent of feeding or starvation commencing after the D_0 thre-

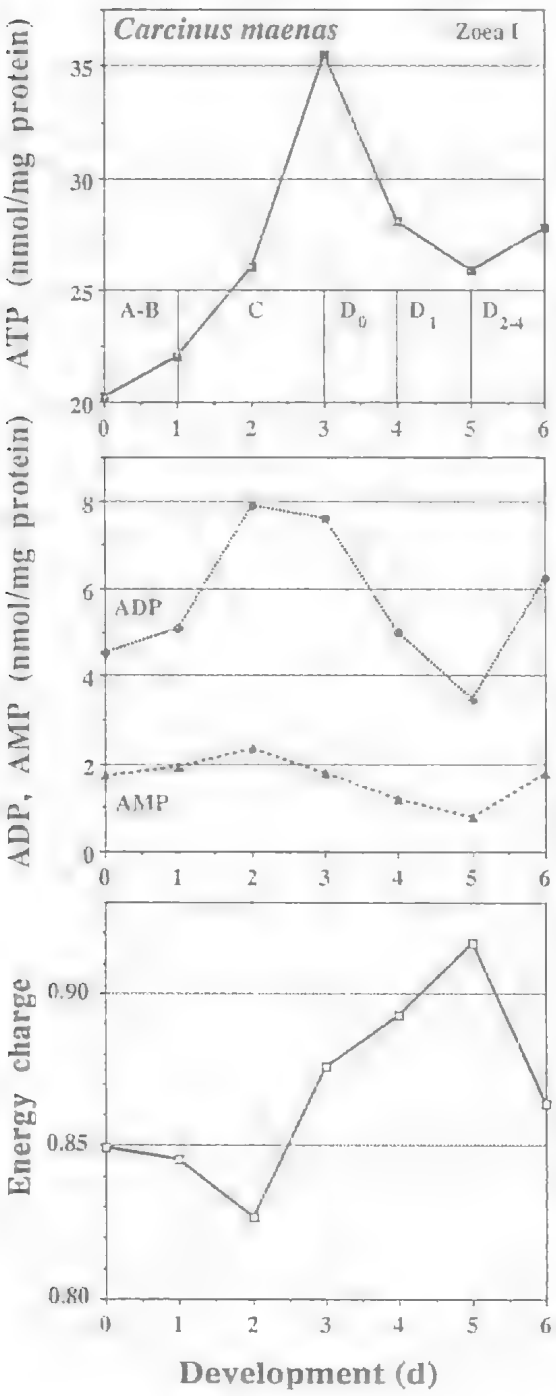

FIG.12 *Carcinus maenas*. Changes in adenosine nucleotide concentrations (ATP, ADP, AMP; nmol ·[mg protein]$^{-1}$) and adenylate energy charge during the moult cycle stages (A–E, cf. Fig. 10) of the zoea I instar (after Harms *et al.*, 1990).

shold (Dawirs, 1983; Anger and Spindler, 1987; Freeman, 1990, 1991; Harms *et al.*, 1990). In the megalopa of *Hyas araneus*, the premetamorphic phase shows particularly strong signs of autonomous development, with reconstruction processes that are associated with drastic losses in the lipid fraction (C/N; Fig. 10), and probably with cell lysis (DNA; Fig. 11).

If high C/N ratios are considered as indicators of a high lipid content and hence, an increased ability to develop without external energy supply, then this index suggests significant differerences in the degree of lecithotrophy among higher taxa of the Decapoda. In Fig. 10, larvae belonging to different infraorders were grouped in a sequence of increasingly advanced taxonomical position (Bowman and Abele, 1982). They show in this order a significant increase in average C/N ratios. This agrees with the tendency of decreasing net growth efficiencies in the same sequence (see above; Fig. 8). Caridean shrimps should reveal, on the average, the lowest degree of lecithotrophy, brachyuran crabs the highest. This tendency corresponds to a decreasing number and variability of instars passed during larval development, and an increasing degree of morphological change in each moult cycle. The latter trend suggests that, as in insects, there may be an evolutionary tendency toward increasingly metamorphic development. While Caridea can respond to unsuitable environmental factors with additional moults and reduced morphogenesis (Knowlton, 1974), the Brachyura are only moderately able to vary their number and morphology of developmental instars, and hence depend more on sufficient energy reserves necessary for drastic reconstruction processes. Thus, bioenergetic traits of larvae may reflect phylogenetic trends, with an increasing degree of lecithotrophy, increasing ecological specialisation, and an increasingly metamorphic type of development in the evolution of the Decapoda.

ACKNOWLEDGEMENTS

Our investigations on the bioenergetics of decapod larvae have been generously supported by the Deutsche Forschungsgemeinschaft (DFG; grants under An 145-1 and -2). I thank all colleagues, technicians, and students who contributed to these studies, with their cooperation, technical assistance and help, respectively. I am grateful to Dr M. Kirchner for correcting the English manuscript.

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